THE EXTRAFASCICULAR CAMBIUM OF CERATOZAMIA

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(WITH PLATE VII)

The anatomical features presented by the seedling of Ceratozamia described in a previous paper (3) gave promise of such phylogenetic importance that the study has been continued upon older stems. The interest centers mainly in the extrafascicular cambium—its origin, its distribution, and its failure to differentiate xylem and phloem which could be clearly recognized as such. In a careful examination of microtome sections of over eighty seedlings, varying in age from a few months to two years, only one small extrafascicular bundle was found.

The origin of the concentric vascular zones of cycad stems puzzled the early anatomists. BRONGNIART (1), failing to distinguish the phloem in these zones, regarded them as the equivalent of the seasonal wood rings of dicotyledons. VON MOHL (8) said that they were an aggregation of bundles which passed out from the central cylinder and, running downward in the cortex, grouped themselves in a ring. LESTIBONDOIS (4) saw individual bundles in the cortex, but thought they foreshadowed the breaking-up of the central stele, and so considered the cycads as a transition group from dicotyledons to monocotyledons. METTENIUS, to whom we are indebted for much of our knowledge of cycad anatomy, made no attempt to explain the extra vascular zones. CONSTANTIN and MOROT (2) thought that the tissue arose from the pericycle.

All the early research was confined to mature stems of Cycas and Encephalartos. In 1890, SOLMS-LAUBACH (7) reported the absence of such zones in *Ceratozamia mexicana*. In 1896 WORSDELL (9) added Macrozamia to the list of cycads in which these thickenings occur, and in 1898 (10) recorded their absence from the stem of Stangeria; in 1900 (11) he found them in the root of *Bowenia spectabilis*. His study of seedlings of species of Cycas (10) demonstrated to WORSDELL that the extrafascicular zones in mature stems arose as independent cortical cylinders arranged in distinct series, the innermost ones being composed of primary tissue. By a later growth of the central cylinder they become appressed to its periphery and flattened radially. This study brought to him and to his readers a conviction of the truth contained in his earlier suggestion that the cycads are closely related to the Medullosae, which are polystelic like the ferns. MATTE's study of *Cycas siamensis* and *Encephalartos Barteri* (5) is an almost perfect demonstration of WORSDELL's theory.

My work upon Ceratozamia will come as cumulative evidence. SOLMS'S statement concerning the absence of extrafascicular zones is correct as far as the seedling is concerned; but the presence of extrafascicular cambium in great abundance led me to make a careful search to discover its relation to the central cylinder. In the study of seedlings described in the previous paper I was unable to do this on account of the disturbances caused by mucilage ducts, which are large, abundant, and irregular in distribution. In the study of older stems I have been more fortunate. Four-year-old seedlings have in the hypocotyl clearly distinguishable rings or cylinders of cambium. The cylinders are arranged in several series. Those of the innermost series, though decidedly flattened, are the most distinct.

Fig. 1 represents diagrammatically a section of the hypocotyl slightly below the exit of the cotyledonary traces. The innermost cylinders (*a*, *b*, *s*) arise in the pericycle near the transition region and are of primary origin. They extend well up in the stem, though pushed outward by the horizontal cotyledonary traces. The other rings appear later. It would seem that the single bundle described in the previous paper (**3**, *fig. 30*, *z*) was differentiated from one of the outermost series of cylinders.

Fig. 2 is a detail of the inner portion of half the section represented in *fig. 1*. One large cambial ring (*a*) is represented, and ends of two others (*b* and *s*). Several small rings (*e*, *r*) suggest how concentric bundles might arise.

The cause of the flattening is manifestly the enlargement of the central cylinder and the consequent pressure upon the inner side of the cortical cylinders (*a*, *b*, *s*). The final result is a central cylinder surrounded by several more or less imperfect zones of cambium cells. The xylem and phloem which these cells might produce would be oriented differently; the xylem on the centripetal side of the zone would be differentiated toward the periphery and the phloem toward the center of the stem. But in many cases, the inner cambium of each zone would cease to function, and we should then have successive zones of alternating xylem and phloem all with normal orientation. Occasionally a bit of the elongated cylinder would be disconnected, the cambium would round out, the growth of xylem would eliminate the pith, and a concentric bundle would result. All these conditions are found in the Medullosae, from the distinct fern-like polystely in *Medullosa Solmsii* and *M. anglica* to the condition of *M. stellata*, which closely resembles *Cycas revoluta*.

I have not yet examined mature stems of plants of this genus. WORSDELL (**9**) has confirmed SOLMS-LAUBACH'S statement that the extrafas-

cicular zones are lacking; but MATTE (6) reports that he saw them in stems which he examined. I am therefore in doubt whether it is an absolute failure to function, or only a delay; in either case we have an indication that the cortical vascular tissue is a disappearing character.

Another feature to which attention should be called is the constant occurrence of centripetal xylem in the cylinder of the hypocotyl and in the bases of the cotyledonary bundles. This is represented in *fig. 28* of the paper already cited and also in *fig. 2* of the present one. It is often relatively more abundant than in some stems of Lyginodendron. The stem cylinder above the cotyledons is endarch, the leaf traces becoming mesarch almost immediately after leaving the cylinder.

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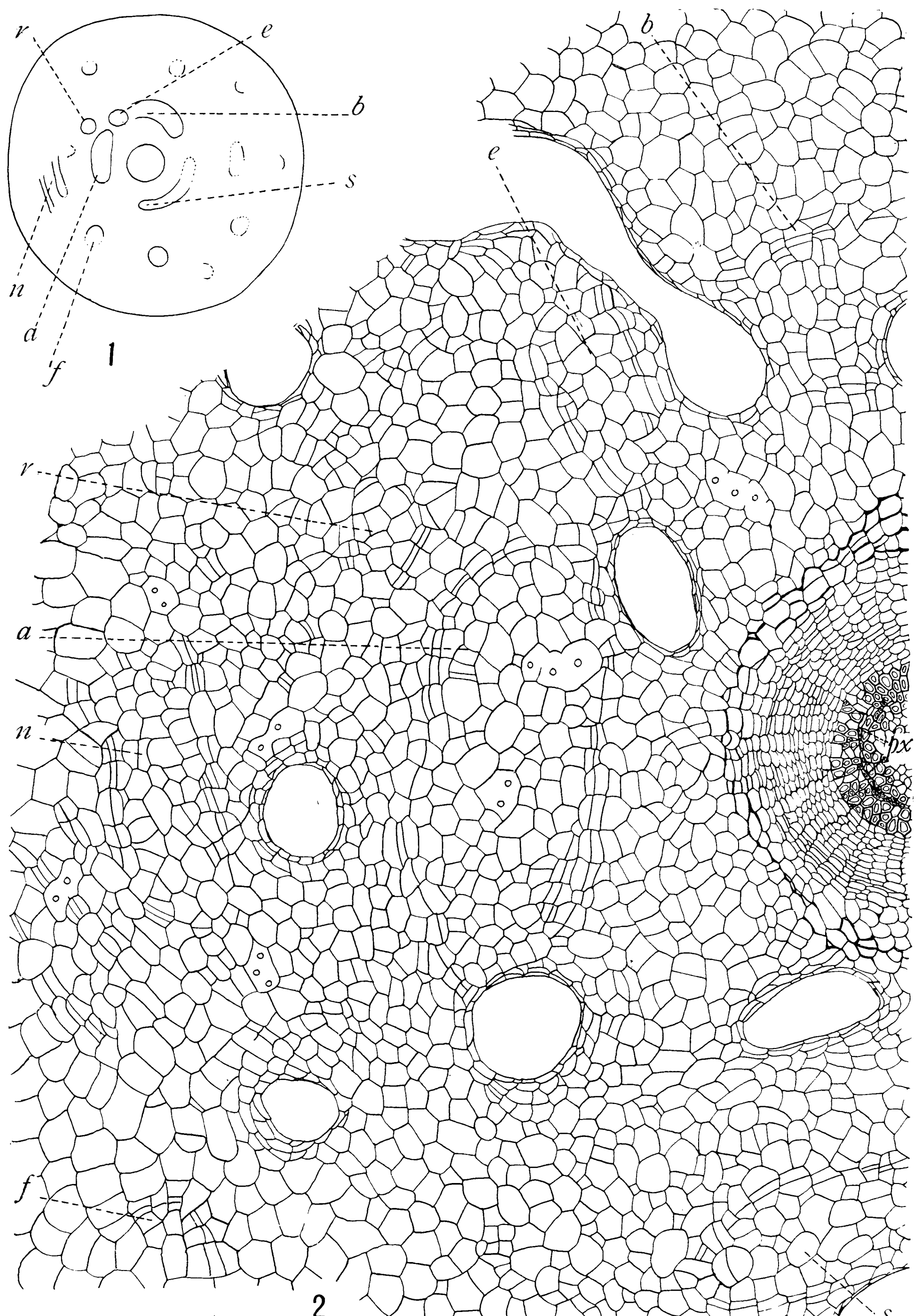

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DORETY on CERATOZAMIA